Feeding Ecology of Eelgrass Fish Communities

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ABSTRACT

The principal components in the diets of fishes utilizing eelgrass (*Zostera marina*) beds in the shallow water estuaries near Beaufort, North Carolina, were detritus, planktonic copepods, and epifaunal crustaceans. Food produced within the eelgrass beds such as eelgrass, crustaceans, gastropods, and detritus, could have accounted for approximately 56% by weight of the diet of the eelgrass fish community.

Pinfish (*Lagodon rhombiodes*) under 35 mm feed primarily on planktonic copepods, thereafter detritus gradually replaced copepods. When pinfish reached a length of about 70 mm they became more omnivorous consuming a greater proportion of plant material and polychaetes. Changes in feeding habits may have been responsible for significant differences in the weight-specific caloric contents observed between three size groups of both pigfish and pinfish.

All species except one did not feed in the beds at night even though biomass of all fish was twice as high at night than during the day.

The eelgrass fish community does not appear to be food-limited because the total annual food production in the beds is greater than the total annual food consumption by the eelgrass macrofauna.

Eelgrass (*Zostera marina*) beds are known to provide food and protection for a variety of animals (Adams 1976; Thayer, Wolfe, and Williams 1975), including many species of juvenile fishes (Carr and Adams 1973; Kikuchi 1961; Hoese and Jones 1963; Godfrey 1970; Hellier 1962; Briggs and O'Connor 1971). Food habits studies of fishes utilizing such areas help to illustrate the role of seagrass beds in fish ecology and also are important in the construction of energy budgets of eelgrass fish communities. Energy budgets indicate the qualitative and quantitative contribution of each food source to the total energy flow of a community and suggest possible trophic relationships between organisms in a community.

The present study was undertaken in connection with investigations of the structural and functional aspects of eelgrass fish communities. Principal objectives of this study were determinations of the following: (1) the main components of the diet and quantities consumed, (2) the importance of food produced within the eelgrass bed to the diet of the major species of fish there and the export of this food into the surrounding estuarine areas, (3) ontogentic changes in diet with growth, and (4) the periodicity of feeding.

METHODS

Fish were collected from two eelgrass beds located in the shallow estuarine systems near Morehead City, North Carolina (Fig. 1). The temporal distribution of the standing crop for each species collected from the eelgrass beds is presented in Adams (1976). For gut analysis, fish were collected each month for a year with a 15.2-m bag seine or a small otter trawl and immediately frozen in the field. In the laboratory, the gut contents (stomach and intestinal) of 2 to 12 (according to seasonal availability) fish of each species and size group were combined, identified, and sorted into major food items with the aid of a binocular microscope. Dry weights of each food category and of each fish were obtained by freeze drying in a lyophilizer. The composition of each food item in the gut was expressed as a percent of dry body weight of fish. All non-green pigmented plant material in various stages of decomposition and all unidentifiable organic remains were, after separation from sand, designated as detritus. Some of this material, however, might have been partially digested plant and animal tissue. Fine organic material, such as that mixed with
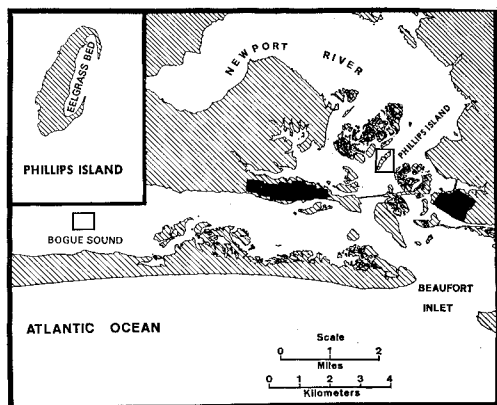
FIGURE 1.—*Newport River and Bogue Sound showing the location (indicated by squares) of the eelgrass beds at Phillips Island and in Bogue Sound.*

mud, was also designated as detritus. The average annual percentage contribution of each food item to the total diet of each species was calculated by averaging the monthly percentage composition of the particular food category in the diet of that species.

Diurnal feeding habits were determined by gut analysis of fish collected at 4-h intervals throughout two 24-h periods.

Caloric determinations on three size groups of pinfish (*Lagodon rhombiodes*) and pigfish (*Orthopristis chrysoptera*) were made each month with a Phillipson oxygen microbomb calorimeter. The average annual caloric content for each size group and species was calculated by summing and averaging the monthly values of the caloric content of organic matter [cal/mg ash-free dry weight (AFDW)]. At least three replicates were run each month for each species and size group for which samples collected that month. Three replicates of each sample produced an average standard error of ±0.11 cal/mg AFDW with 95% confidence limits of the mean of ±0.47 cal/mg AFDW. Organic contents of freeze-dried samples were measured by loss of weight following ashing at 500 C for 36 h.

RESULTS

Detritus was the most important food item in the diets of juvenile pinfish and pigfish, adult pinfish, spot (*Leiostomus xanthurus*),

and filefish (*Monacanthus hispidus*) (Table 1). Most of the plant detritus in the gut could not be separated into eelgrass and non-eelgrass detritus, but likely was predominantly of eelgrass origin since during most of the year decaying eelgrass blades were abundant on the surface of the sediment within the eelgrass bed (Adams 1974). Planktonic copepods were the most important dietary items of silversides (*Menidia menidia*) and mojarra (*Eucinostomus gula*), and made up one-half of the diet of anchovies (*Anchoa* sp.) (Table 1). Calanoid copepods also made up a large part of the annual ration of juvenile pinfish and pigfish, silver perch (*Bairdiella chrysura*), and pipefish (*Syngnathus* sp.). Juvenile and larval fishes contributed to the diet of silversides, silver perch, oyster toadfish (*Opsanus tau*), and flounders (*Paralichthys* sp.). Polychaetes were fairly important in the diet of adult pinfish, silver perch, and spot. Crustaceans such as the gammarid and caprellid amphipods, isopods, *Hippolyte*, *Palaemonetes*, and small blue crabs (*Callinectes sapidus*) made up a large portion of the diet of silver perch, pipefish, flounder, and the gag grouper (*Mycteroperca microlepis*) (Table 1). These four fish appeared to be primarily carnivorous throughout most of their life. Pinfish, especially the larger individuals, were omnivorous, and evidently consumed any food available (Table 1). Intact whole bay scallops (*Argopecten irradians*) and the small gastropod, *Bittium varium*, made up 95% and 50% of the diet of the striped burrfish (*Chilomycterus schoepfi*) and the oyster toadfish, respectively. Bay scallops as large as 2.5 cm and as many as 450 *Bittium* were found in the guts of the burrfish and toadfish, respectively. Undigested eelgrass, eelgrass seeds, and filamentous algae made up 18% and 23% of the diet of juvenile and adult pinfish, respectively (Table 1), but this plant material probably provided no nutritional value to these fish.

Food material produced within the eelgrass beds, such as eelgrass and its epiphytes, gammarid and caprellid amphipods, *Hippolyte*, *Palaemonetes*, *Bittium*, and the bay scallop, contributed 35% by weight of the total annual diet of the eelgrass fish community. Assuming that all the detritus consumed by the fish

TABLE 1.—*Annual average percentage by weight of each food item in the diet of the major species of fish inhabiting eelgrass beds. Number of samples shown in parentheses.*

Food item	Juvenile pinfish (118)	Adult pinfish (97)	Juvenile pigfish (105)	Silversides (130)	Silver perch (77)	Spot (112)	Pipefish (61)
Detritus	30.4	27.8	46.2	4.1		67.5	
Calanoid copepods	19.6	9.5	35.2	73.1	18.5	0.8	37.5
Polychaetes	3.9	10.5	0.6		13.7	6.0	
Gammarid amphipods	10.9	7.2	1.2	5.5	16.8	2.6	12.5
Caprellid amphipods	6.3	9.5		3.3			31.0
Filamentous algae	7.1	9.8			2.5	0.5	
Eelgrass	10.5	7.7			5.0	1.0	
Eelgrass seeds		5.8					
Pelecypods		0.2	0.4			14.2	
Bittium		0.5		1.0	2.5		
Isopods	0.6	0.5					
Palaemonetes	3.6	0.8	12.5		7.5	0.3	
Juvenile and larval fish		0.8		12.3	15.0		
Crabs	0.7		1.8				
Scallops		1.7					
Hippolyte	3.0	0.7	0.6	0.3	18.5		19.0
Harpacticoid copepods	1.7	0.5	1.5			3.3	
Other[a]	1.7	6.5		0.4		3.8	

Food item	Burrfish (26)	Filefish (87)	Anchovy (90)	Gag (26)	Mojarra (65)	Toadfish (28)	Flounders (39)	% of total
Detritus		65.5	50.0				1.7	21.7
Calanoid copepods			50.0		100.0			24.6
Polychaetes		0.5						2.5
Gammarid amphipods							1.8	4.2
Caprellid amphipods								3.6
Filamentous algae						3.8		1.7
Eelgrass		12.5				3.7		2.9
Eelgrass seeds								0.4
Pelecypods								1.1
Bittium	82.5					25.0	30.0	10.2
Isopods								0.1
Palaemonetes				50.0				5.3
Juvenile and larval fish	5.0			6.0		37.5	41.5	8.4
Crabs						5.0	25.0	2.3
Scallops	12.5					25.0		2.8
Hippolyte				44.0				6.2
Harpacticoid copepods		5.0						0.9
Other[a]		6.5						1.4

[a] Includes: seaweed, brittle stars, bryozoans, nematodes, nemertines, flatworms, nauplii, and megalops stages of crustacea.

community was of eelgrass origin, then up to 56% by weight of the diet of the eelgrass fish community was produced within the bed.

The feeding habits of pinfish and pigfish appeared to change with size (growth). In April and May, when the population of pinfish and pigfish consisted mainly of post-larvae and juvenile (15 to 30 mm standard

TABLE 2.—*Monthly variations in the percentage of food items consumed by juvenile pinfish (1), juvenile pigfish (2), and adult pinfish (3) in the eelgrass beds.*

Food item	Jan. 1	Feb. 1	Mar. 1	Apr. 1	Apr. 3	May 1	May 2	May 3	June 1	June 2	June 3	July 1	July 2	July 3	Aug. 1	Aug. 2	Sep. 1	Sep. 2
Detritus				9	14	20		26	46	43	43	54	60	43	80	43	64	85
Calanoid copepods	22	31		53	24	66	100	14	54	57		1	19					
Polychaetes	18			7	1			5			2		2	30		1		
Gammarid amphipods	9	25	75		12			17					6				14	4
Caprellid amphipods	7	19	25	12	32			6						14				
Filamentous algae	44	25		2	13			8			4			16			3	
Eelgrass					1			5			10	1					3	
Eelgrass seeds								6			17							
Pelecypods											1		2					
Bittium											2							
Isopods								2				4						
Palaemonetes								3				3			20	47	8	15
Juvenile and larval fish											3							
Crabs																9	7	
Scallops											7							
Hippolyte				7	1			2				23	3					
Harpacticoid copepods				7	2	10							8					
Seaweed				1				4			9							

TABLE 3.—*Caloric content of organic matter (per mg of whole body tissue) for three size groups of pinfish and pigfish. Each sample (N) represents the average of 3–4 replicates. Significant differences at the 0.05 level between a given size group and the largest size group within each species is indicated by an asterisk (*).*

Species	Size (mm)	N	cal/ mgAFDW	± SD
Pinfish	>89	39	5.91	0.34
Pinfish	51–85	87	5.54*	0.27
Pinfish	20–50	48	5.46*	0.25
Pigfish	>86	36	5.85	0.38
Pigfish	38–82	31	5.52*	0.32
Pigfish	16–38	20	5.48*	0.26

length) (Adams 1974), the main food item was planktonic copepods, with detritus making up a lesser proportion of the diet (Table 2). Throughout the spring and summer, as the pinfish and pigfish grew larger, copepods became less important. At an average standard length of 35 mm (in mid-June), the composition of the diet of juvenile pinfish and pigfish was divided about evenly between detritus and copepods (Table 2). Pinfish began to feed less on detritus as they reached a length of 65 to 70 mm, and then assumed a more omnivorous feeding habit with polychaetes, plant material (eelgrass, eelgrass seeds, algae), and larval fish making up an increasingly larger percentage of the diet. The variation in food habits of the pigfish as it grows seems to demonstrate the same pattern followed by pinfish, although not enough of the larger pigfish (>80 mm) could be collected during the year to confirm this. The high percentage of benthic detritus (Table 1), sand, and mud ingested by spot and filefish indicated that they were mainly benthic feeders. There was also a change in the weight-specific caloric content of pinfish and pigfish with size. Both the larger pinfish and pigfish had significantly higher caloric content of organic matter than the two smaller size groups of each of these two species (Table 3).

The pattern of feeding throughout two 24-h periods for some of the major species inhabiting the eelgrass beds is shown in Figure 2. Each species fed mainly during the daylight hours except for silver perch, which fed primarily at night. The peak time of occurrence of food material in the gut (and thus, the
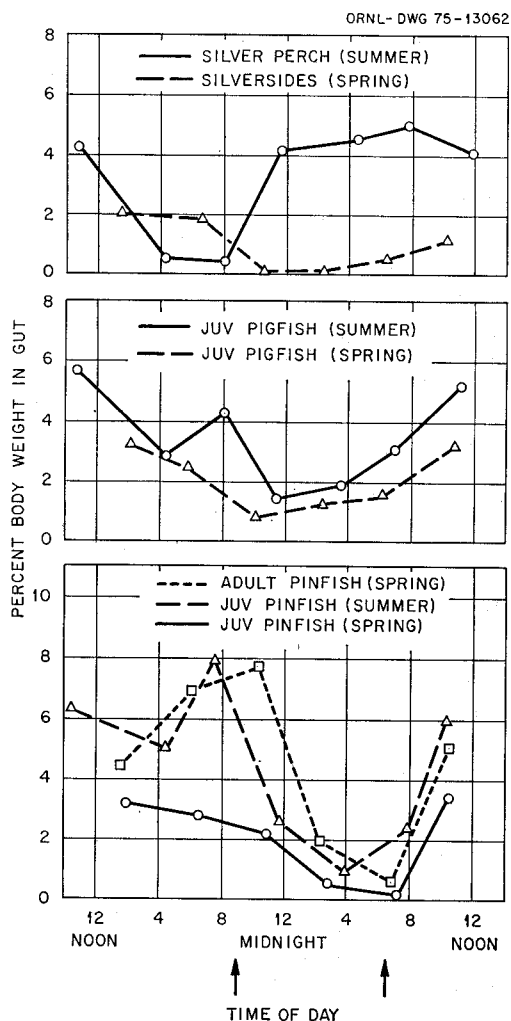

FIGURE 2.—*Periodicity of feeding for juvenile pinfish and pigfish, adult pinfish, silver perch, and silversides. Arrows represent sunset and sunrise.*

main feeding periods) for the other species generally occurred around dusk. Their guts were almost empty shortly before dawn.

DISCUSSION

Three main trophic groups are represented within the eelgrass fish community. Carnivores include silversides, silver perch, pipefish, flounder, and the gag; the detritivores include spot and filefish; and the omnivores include pinfish and pigfish. This division of feeding relationships also changes with de-

velopmental stage (Table 2). The utilization of a wide variety of available foods and separation of feeding niches might, in part, explain the high annual average biomass (1.5 gDW/m^2) and production (4.5 gDW/m^2) (Adams 1976) of the eelgrass fish community compared to other marine communities reported in the literature.

The general trend in the feeding habits of the pinfish as it grows throughout the year, appears to be a dominance of planktonic copepods in the diet until the pinfish reach a length of about 35 mm, followed by a gradual replacement of copepods by detritus, and finally, an omnivorous stage is reached around 70 mm at which time an increasingly larger percentage of polychaetes and plant material is consumed. Carr and Adams (1973) found a similar pattern of feeding for 36- to 70-mm pinfish inhabiting seagrass beds in Florida. The 36- to 70-mm size groups consumed mainly epiphytes, while the 60- to 80-mm size group fed more omnivorously on epiphytes, shrimp, and fish. In this study, the change from a predominate copepod-detritus diet to a more omnivorous diet with smaller proportions of detritus may account for the significant differences in weight-specific caloric content between the three size groups of both pigfish and pinfish (Table 3). It seems reasonable to speculate that changes in feeding habits may have been responsible for the relatively higher weight-specific caloric contents of the larger pinfish and pigfish since changes in feeding habits and significant changes in the caloric content of organic matter occurred at about the same stage of growth (size). Thayer et al. (1973) found that carbon, caloric, and lipid contents of pinfish began to increase when these fish reached a length of about 65 mm, and Prus (1970) stated that intraspecies differences in caloric content are a result of food conditions, developmental stage, or physiological state.

Studies on periodicity of feeding indicated that except for silver perch, the major species of fish within the eelgrass bed were not feeding in the bed at night. In a previous study (Adams 1976) the biomass of fish within the bed at night was found to be twice the day biomass (2.03 and 1.1 gDW/m^2 during the

night and day, respectively). The higher biomass of fish within the bed at night, therefore, cannot be explained by fishes migrating into the bed to feed. A reasonable explanation for higher night biomass is that high water temperatures during the day cause fish to migrate out of the bed (especially during the summer) and that only during the night when temperatures drop several degrees do the fish migrate back into the bed (Adams 1976). Sampling bias due to net avoidance was probably minimal because of the nature of the sampling equipment used and the turbid estuarine water in the sampling areas. The drop-net described by Adams (1976) to sample the eelgrass fish community was used in shallow water (usually less than 1 m deep), and due to the rapid descent of the net through the water column allowed little time for fish escapement.

Two studies have shown that higher abundances of some species of fish at night in shallow water areas are probably not related to feeding activities. McCleave and Fried (1975) found that high nocturnal densities of alewife/blueback herring (the dominant nighttime fish) in a shallow estuarine cove probably resulted from movement into shallow water unrelated to feeding. Emery (1973) working in a shallow area of an Ontario lake, reported that the number of fish apparent at night in shallow water was greater than in the daytime, primarily because of the influx of offshore species which was due to a lack of cover in offshore areas for these resting diurnal species.

The basis of the fish food chain in the eelgrass bed is probably detritus and its associated microbial community. A study by Thayer, Adams, and LaCroix (1975) found that of the 21,400 kcal/m^2 of plankton, benthic algae, eelgrass, detritus, bacteria, and invertebrates potentially available annually to the consumers in the Phillips Island bed, detritus (seston, particulate detritus less than 1 mm and to a depth of 18 cm in the sediment) made up 21,160 kcal/m^2 or over 99% of this. Even though only 21% of the total food energy consumed by the total fish community is taken in directly as detritus (Table 1), the invertebrates consumed by the fish community are

primarily detrivores. Adams and Angelovic (1970) found that *Palaemonetes*, *Bittium*, and *Glycera*, which are abundant in the eelgrass beds, can utilize detritus and its associated microorganisms as an energy source. Odum (1971) also reported that the major invertebrate detritus consumers in a Florida estuary were the principal food items of the majority of the carnivorous fish in the estuary. Carr and Adams (1973) also suggested that detritus may serve as an energy base for fishes that inhabit seagrass beds in Florida. Thayer, Adams, and LaCroix (1975) estimated that the macrofauna in the Phillips Island eelgrass bed consumed an amount of energy equivalent to 55% of the net production of eelgrass, phytoplankton, and benthic algae in the bed. This suggests, therefore, that none of the organismal compartments such as the fish community in the eelgrass beds in the vicinity of the study appear to be food-limited. This further suggests that there is an excess of plant production in the eelgrass system which is likely accumulated in the sediments to a certain degree and also exported to the adjoining estuary, thus providing detrital materials to the system (an energy equivalent to 45% of the net production of eelgrass, phytoplankton, and benthic algae in the bed). This export may be highly significant to the trophic function of the shallow estuarine systems in the area since eelgrass is estimated to supply as much as 64% (Williams 1973) of the total primary production in the system.

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